Monophyly of the genus *Liopsetta* (Pleuronectidae)

by

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Abstract. – A phylogenetic analysis of 15 flatfish species based on 40 morphological characters was conducted to determine the interrelationships of the genera *Liopsetta*, *Pleuronectes* and *Pseudopleuronectes*. The results indicate that *Liopsetta* forms a monophyletic lineage defined by the reduction of the infraorbital sensory canal of the ocular side, small scale size and small body size. The monophyly of *Pseudopleuronectes* (including *P. obscurus*) is supported by the interrupted coronal commissure and of *Pleuronectes* by the presence of radii surrounding entirely the focus of scales and the absence of scleral bones. The synapomorphies of *Pleuronectes* and *Liopsetta* support the hypothesis that these genera are distinct and valid. The relationships of the three species of *Liopsetta* were incompletely resolved.

Résumé. – La monophylie du genre *Liopsetta* (Pleuronectidae).

Une reconstruction de la phylogénie de 15 espèces de poissons plats fondée sur 40 caractères morphologiques a été menée pour déterminer les relations de parenté des genres *Liopsetta*, *Pleuronectes* et *Pseudopleuronectes*. Les résultats indiquent que *Liopsetta* forme un groupe monophylétique défini par la réduction du canal sensoriel infraorbitaire, la taille réduite des écailles et une taille corporelle également réduite. La monophylie de *Pseudopleuronectes* (*P. obscurus* inclus) est soutenue par la présence d'une commissure coronale interrompue, et celle de *Pleuronectes* par la présence de radii recouvrant complètement le foyer de l'écaille et l'absence d'os scléraux. Les synapomorphies des genres *Pleuronectes* et *Liopsetta* soutiennent l'hypothèse de validité pour ces genres. Les relations de parenté des trois espèces du genre *Liopsetta* sont incomplètement résolues, mais aucune donnée ne corrobore la conspécificité de *L. glacialis*, *L. putnami* et *L. pinnifasciata*.

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Received: 20 Nov. 2013
Accepted: 27 Jan. 2014
Editor: J.Y. Sire

Key words

Pleuronectidae
Liopsetta
Taxonomy
Monophyly
Morphology

The dextral flatfish species of the genus *Liopsetta* (family Pleuronectidae) inhabit arctic seas and boreal seas of Atlantic and Pacific oceans. They occur in estuarine brackish waters and frequently enter freshwaters. These small and uncommon species are of minor commercial importance (Andriashev, 1954; Fadeev, 2005).

The taxonomic status of the genus *Liopsetta* Gill, 1864 has been questioned several times in the last decades. *Liopsetta* was erected by Gill (1864) for the species *Platessa glabra* Storer, 1843 sampled in Boston harbour, Massachusetts. This binomial name was preoccupied by *Platessa glabra* Rathke, 1837 from the Black Sea, which was relegated later by Berg (1932) to synonymy of *Platichthys flesus* (L., 1758). Gill (1864) created the new combination *Liopsetta glabra* and in the same paper described the new genus and species *Euchalarodus putnami* from Salem, Massachusetts. Later Bean (1879) demonstrated that *E. putnami* was in fact the male of *L. glabra*; Jordan and Goss (1889) confirmed this view, and also stated that there was no difference between *L. glabra* and *Pleuronectes glacialis* Pallas, 1776. Norman (1934: 368) discussed the taxonomy of these species (Bean, 1879; Jordan and Goss, 1889; Hubbs, 1915). He relegated four species – *L. glacialis*, *L. putnami*, *L. pinnifasciata* (Kner *in* Steindachner and Kner, 1870) and *L. obscura* (Herzenstein, 1890) – to the genus *Liopsetta*, hypothesizing that the first three species were very closely related and that *L. obscura* was similar to *Pseudopleuronectes*.

Sakamoto (1984) encompassed *Liopsetta* and five other genera into the genus *Pleuronectes* mainly on the basis of osteology. This decision was controversial (Rass, 1996) and as a compromise, *Liopsetta* was considered later as the subgenus of *Pleuronectes* (Lindberg and Fedorov, 1993). Cooper and Chapleau (1998) conducted a cladistic analysis of 106 characters of 53 pleuronectid species and put *L. glacialis, L. putnami* and *L. pinnifasciata* within the genus *Pleuronectes* and *L. obscura* within *Pseudopleuronectes a posteriori*. Voronina and Evseenko (2001) reported morphological differences between *Liopsetta*, *Pleuronectes* and *Pseudopleuronectes*, but these data were not compared with other pleuronectid characters, i.e. tested within a phylogenetic framework. Now *Liopsetta* is considered either a valid genus (Froese and Pauly, 2013) or a synonym of *Pleuronectes* (Roje, 2010; Froese and Pauly, 2013; Nakabo, 2013).

The specific aims of this paper are to investigate the monophyly of the genus *Liopsetta* and evaluate its relationships to *Pleuronectes* and *Pseudopleuronectes*, adding diag-

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Cybium 2014, 38(1): 43-52.

noses of these genera and descriptions of *Liopsetta* species.

MATERIAL AND METHODS

Measurements follow Hubbs and Lagler (1958). Length, in mm, is standard length (SL). Institutional codes follow Leviton *et al*. (1985). Staining sensory canals by methylene blue followed Ueno (1970) and the terminology adopted for lateral line system of bony fish of Webb (1989) and Mandritsa (2001) were used. Some specimens were cleared and stained with alizarin in order to study osteological characters. Drawings are based on photographs obtained via Nikon Coolpix 5000 digital camera and microscope. The literature data on the maximum body size, egg size and larva pigmentation are presented in table I.

Specimens examined

Fifteen pleuronectid species were examined, including three species of *Liopsetta*, eleven representatives of tribe Pleuronectini *sensu* Cooper & Chapleau, 1998, and *Verasper variegatus* (Temminck & Schlegel, 1846). The following list includes all specimens (spms) utilized in the phylogenetic analysis: *Limanda aspera* (Pallas, 1814): 6 spms, 235-270 mm SL ZIN 8731, 19075, 45171; *L. limanda* (L., 1758): 17 spms, 51-280 mm SL ZIN 3544a, 8782, 19198, 51731, 52209; *L. proboscidea* Gilbert, 1896: 4 spms, 140-165 mm SL ZIN 18165, 33462, 52895; *Liopsetta glacialis*: 67 spms, 90-180 mm SL ZIN 8514, 9763, 9961, 11141, 11149, 18895, 19083, 19084, 19087, 19089, 41418, 43736, 45198, 46526, 46546, 47005, 49985, USNM 028618, 029913, 032905, 033839, 034037, 049122, 070951, 077139, 084584; *L. pinnifasciata*: 22 spms, 73-210 mm SL ZIN 12373, 13077, 13175, 19184, 19913, 36154, 45200, NMW 42643 (holotype); *L. putnami*: 13 spms, 54-200 mm SL ZIN 5918, USNM 53681, 53682, 126828, 165256 (syntypes), 165257, 154786, 165255, MCZ 30910, 56446; *Platichthys flesus*: 15 spms, 65-265 mm SL ZIN 3140, 3301, 3384, 18770, 27163, 35243, 43685, 51555, 51556; *P. stellatus* (Pallas, 1788): 15 spms, 85-265 mm SL ZIN 45090, 45595, 45599, 45600, 45631, 45632, 46527; *Pleuronectes platessa*[1] L., 1758: 15 spms, 105-165 mm SL ZIN 45152, 50834, three unregistered spms, 330-360 mm SL; *P. quadrituberculatus* Pallas 1814: 6 spms, 130-490 mm SL ZIN 13134, 34757, 45151; *Pseudopleuronectes americanus* (Walbaum, 1792): 6 spms, 175-265 mm SL ZIN 23693; *P. herzensteini* (Jordan & Snyder, 1901): 5 spms, 153-280 mm SL ZIN 47062, 17720; *P. obscurus* (Herzenstein, 1890): 18 specimens, 68-323 mm SL ZIN 8726 and 8727 (syntypes), 19059, 25957, 26281, 26283, 29082, 34679, 43731; *P. yokohamae*[2] (Günther, 1877): 11 spms, 127-300 mm SL ZIN 8879, 12377, 42874, 47063; *Verasper variegatus*: 2 spms, 270 and 320 mm SL ZIN 55522.

Cladistic procedure

The main aim of the analysis was to estimate the relationships of *Liopsetta* (*L. glacialis, L. putnami, L. pinnifasciata*) and *Pleuronectes* (*P. platessa, P. quadrituberculatus*). The closely related genera *Pseudopleuronectes* (with four species *P. americanus, P. herzensteini, P. obscurus, P. yokohamae*), *Platichthys* (two species *P. flesus, P. stellatus*) and

Table I. - Egg size, postanal larval pigmentation and maximum body size of pleuronectid species. [1]: Pertseva-Ostroumova, 1961; [2]: Laroche, 1981; [3]: Munk and Nielsen, 2005; [4]: Russel, 1976; [5]: Cole and Johnstone, 1902; [6]: Pearcy, 1962; [7]: Fukuhara, 1988; [8]: Yusa, 1971; [9]: Aritaki *et al*., 2001; [10]: Nikolaev, 1958; [11]: see explanation in the text; [12]: Robins and Ray, 1986; [13]: Lindberg and Fedorov, 1993.

Species	Egg size (mm)	Number of postanal pigment bandings	Body maximal length (mm)
Liopsetta glacialis	1.20-1.70[1]	1[1]	330[10]
L. pinnifasciata	1.43-1.61[1]	1[1]	350[11]
L. putnami	1.10-1.40[2]	1[2]	300[12]
Limanda aspera	0.76-0.88[1]	absent[1]	490[13]
L. limanda	0.60-1.20[3, 4,]	absent[5]	400[14]
L. proboscidea	0.72-0.87[1]	absent[1]	400[13]
Pleuronectes platessa	1.63-2.20[3, 4, 5]	absent[3, 4, 5]	1000[13]
P. quadrituberculatus	1.67-2.21[1]	absent[1]	620[13]
Pseudopleuronectes americanus	0.80[2, 6]	1[2, 6]	640[13]
P. herzensteini	0.72-0.92[1]	3[1]	560[13]
P. obscurus	0.78-0.94[1]	2[1]	560[13]
P. yokohamae	0.74-0.86[1, 7, 8]	2[1, 7, 8]	500[13]
Platichthys flesus	0.82-1.13[3, 4]	1[5]	600[13]
P. stellatus	0.97-1.28[1, 8]	1[1, 8]	900[13]
Verasper variegatus	1.77 ± 0.02[9]	heavy pigmentation[1, 9]	600[13]

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[1] Cooper and Chapleau (1998) changed the specific epithet of *Pleuronectes platessa* to *platessus* to agree in gender with *Pleuronectes* and this combination is also used by Roje (2010). However, 'platessa' exists as a noun ('plaice' in Latin) and cannot be changed. Therefore *P. platessa* must be retained.

[2] *P. yokohamae* includes *P. schrenki* as a junior synonym according to recent morphological and genetic data (Vinnikov *et al*., 2006; Kartavtsev *et al*., 2007).

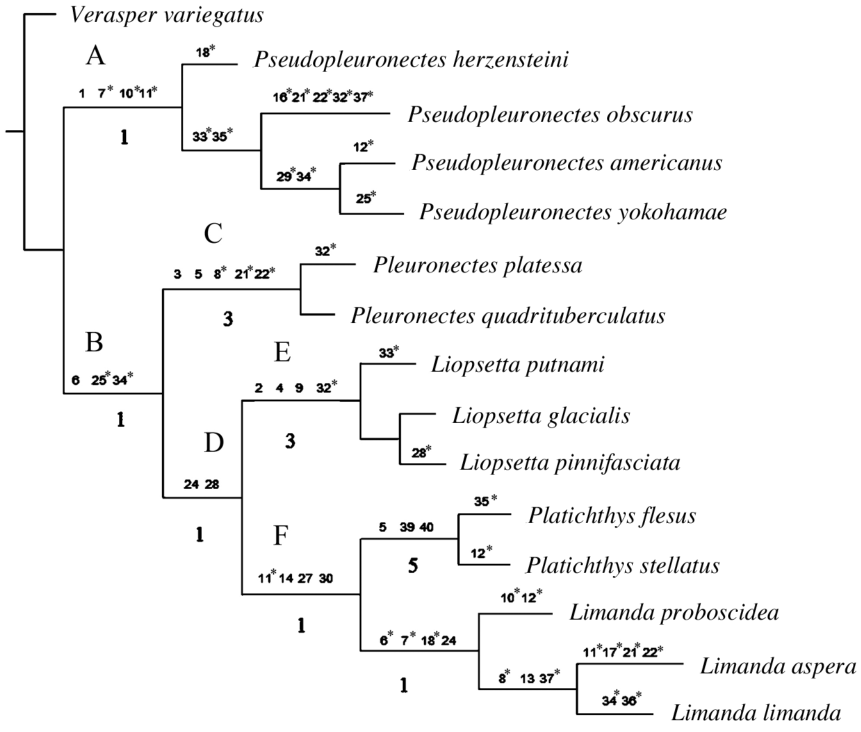

Figure 1. - Strict consensus of three cladograms of relationships among 15 species of flatfishes family Pleuronectidae as produced by the phylogenetic analysis based on the characters coded as listed (Appendix I) and as presented in a data matrix (Appendix II). L 95, CI 0.56, RI 0.68. Letters above branches indicate nodes as described in the text, numbers above nodes indicate character number, asterisk indicates character state reversal, numbers below nodes indicate Bremer support. Outgroup taxon representing *Verasper variegatus*.

Limanda (three species *L. aspera, L. limanda, L. proboscidea*) were included in the phylogenetic analysis, based on the hypothesis proposed by Cooper and Chapleau (1998) and subsequently corroborated in part by other authors (Kartavtsev *et al.*, 2007; Roje, 2011). *Verasper* (based on *V. variegatus*) was used as the outgroup.

The morphological data of Cooper and Chapleau (1998) was reanalysed. Thirty three characters of their analysis were used. Eight new characters and missing data for *Pseudopleuronectes obscurus* and *Platichthys quadrituberculatus* were added. Coding of some characters was changed (see comments for characters in Appendix I). The characters coded in the 15 taxa by 40 character data matrix, Appendix II, form the data used in a parsimony analysis of studied pleuronectids. The distribution of these characters among taxa is presented in the data matrix of Appendix II. The phylogenetic analysis program PAUP* 4.0 (Swofford, 2003) was used to analyse the matrix under the principle of parsimony. All characters were unordered and unweighed, and both binary and multistate characters were used. Resulting trees were rooted at the outgroup, *V. variegatus*. Bremer support of the clades was computed with PRAP 2.0b3 (Müller, 2004).

RESULTS

Analysis of the character set yielded three equally parsimonious cladograms, each with a length of 95 steps, consistency index (CI; Kluge and Farris, 1969) of 0.56 and retention index (RI; Farris, 1989) of 0.68 were recovered using the parsimony ratchet (Nixon, 1999), set at 100 replications. The strict consensus of these three trees is shown in figure 1.

Node A (=*Pseudopleuronectes*) is supported by one unique synapomorphy (character 1-1, coronal commissure interrupted, Figs 2, 3) and three homoplastic synapomorphies (7; 10; 11).

Node B (=sister-group of *Pseudopleuronectes*) is supported by one synapomorphy (6-1, length of pyloric caeca equal or less diameter of pyloric part of stomach, Fig. 4) with a reversal in *Limanda* and two homoplastic synapomorphies (25; 34).

Node C (=*Pleuronectes*) is supported by two unique synapomorphies (3-1, scleral ossicles absent, 5-1 radii completely surrounding focus of scale, Fig. 5C) and three homoplastic synapomorphies (8, 21, 22).

Node D (=sister-group of *Pleuronectes*) is supported by two synapomorphies (24-1, anterior margin of mesethmoid is thin plate, 28-1, teeth on ocular-side dentary fewer than blind-side teeth but greater than 6).

Node E (=*Liopsetta*) is supported by three unique synapomorphies (2-1, reduced infraorbital canal, Figs 2, 6; 4-1, common scales are a half of lateral line scale size, Fig. 5A, B; 9-1, small maximum body length, Tab. I) and one homoplastic synapomorphy (32).

Node F (=*Platichthys-Limanda*) is supported by three synapomorphies (14-1, dentition of near equal or equal

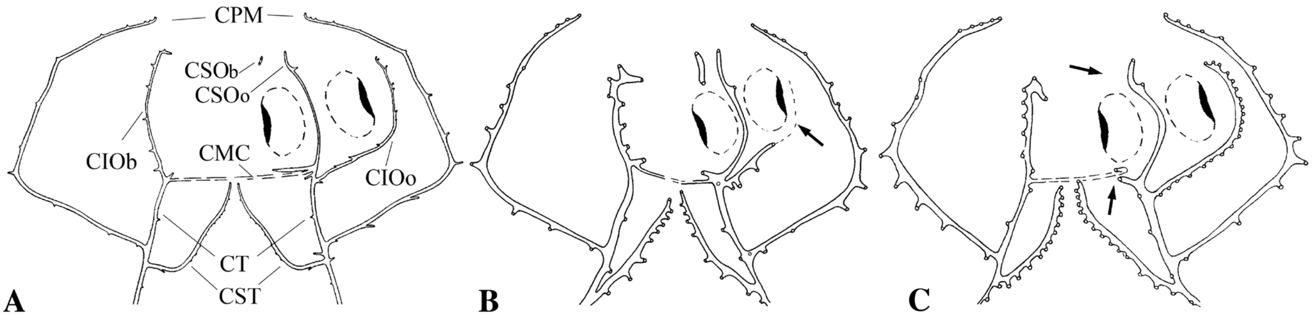

Figure 2. - Scheme of the lateral line canals of the head. **A**: *Pleuronectes*. **B**: *Liopsetta*. Arrow indicates reduced infraorbital canal of the ocular side. **C**: *Pseudopleuronectes*. Arrows indicate interrupted coronal commissure and absence of canal segment in nasale of the blind side. CIOb: infraorbital canal of blind side; CIOo: infraorbital canal of ocular side; CMC: coronal commissure; CPM: preoperculo-mandibular canal; CSOb: supraorbital canal of blind side; CSOa: supraorbital canal of ocular side; CST: supratemporal canal; CT: temporal canal.

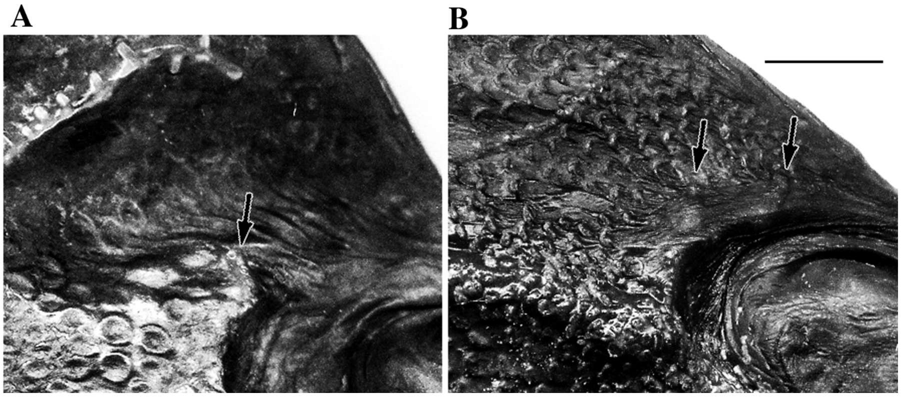

Figure 3. - Ocular side of the head. **A**: *Pleuronectes quadrituberculatus* 375 mm SL. **B**: *Pseudopleuronectes obscurus* 220 mm SL. Arrows indicate pore(s) of the coronal commissure. Scale bar = 1 cm.

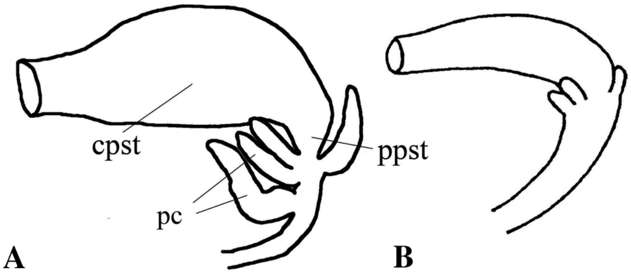

Figure 4. - Scheme of the stomach and pyloric caeca. **A**: *Verasper variegatus*. **B**: *Liopsetta pinnifasciata*. cpst: cardial part of stomach; ppst: pyloric part of stomach; pc: pyloric caeca.

length; 27-1, ocular-side teeth fewer than blind-side teeth but greater than 6; 30-1, bluntly conical teeth or with truncated tips) and one homoplastic synapomorphy (11).

DISCUSSION

The present analysis leads to a new hypothesis of the relationships among *Liopsetta*, *Pleuronectes* and *Pseudopleuronectes*. These conclusions concern the monophyly of the genus *Liopsetta,* its relationship with other genera, and intra-relationships within the genus.

Monophyly of genus *Liopsetta*

The monophyly of *Liopsetta* is well supported (Bremer support 3) and is confirmed by three synapomorphies: reduction of the infraorbital canal of ocular side, small scale size and small maximum body length.

1. The reduction of the infraorbital canal of ocular side, character 2, is characteristic of the genus *Liopsetta* (Voronina and Evseenko, 2001). This character state is rare among pleuronectids (Voronina, 2009) and was not described for *Liopsetta* in previous works (Sakamoto, 1984; Cooper and Chapleau, 1998) although it is clearly visible even in whole preserved unstained specimens (Fig. 6).

2. The small size of scales, character 25, is another synapomorphy of *Liopsetta* species. The genus *Liopsetta* was originally described as having a perfectly smooth body (Storer, 1843; Gill, 1864), because of the small size and number of scales. Considerable individual and ontogenetic variability in scale development exists for the species of this genus (Jordan and Goss, 1889; Schmidt, 1904; Probatov, 1940; Voronina and Evseenko, 2001) with a total absence of scales in three of 67 specimens of *L. glacialis* (present study). The size of the scales has already been used in cladistic analyses of other teleost groups (e.g., Richards and Jones, 2002). However considerable individual and interspecific variability in the absolute size of scale in teleosts, includ-

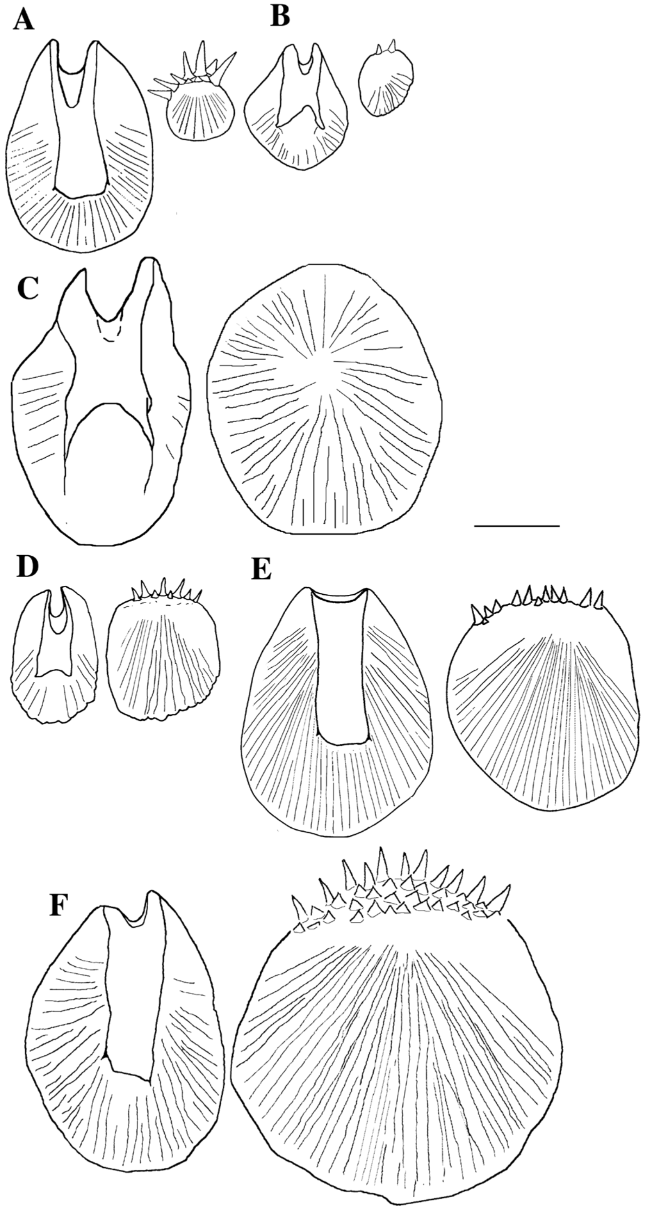

Figure 5. - Lateral line scales and normal scales. **A**: *Liopsetta glacialis*, 155 mm standard length (SL). **B**: *L. putnami*, 145 mm SL. **C**: *Pleuronectes platessa*, 360 mm SL. **D**: *Pseudopleuronectes americanus*, 145 mm SL. **E**: *P. obscurus*, 220 mm SL. **F**: *Verasper variegatus*, 320 mm SL. Scale bar = 1 mm.

ing the Pleuronectiformes (Batts, 1964), makes it difficult to use as a character. Meanwhile the ratio of scale size and the size of the lateral line scales is characteristic for some taxa, as demonstrated in Centrarchidae (Branson and Moore, 1962). According to our data, common scales, i.e. not lateral line scales, are equal in size or larger than the lateral line scales in all pleuronectids studied here except *Liopsetta*. In *Liopsetta*, the common scales are half the size of lateral line scales (Fig. 5).

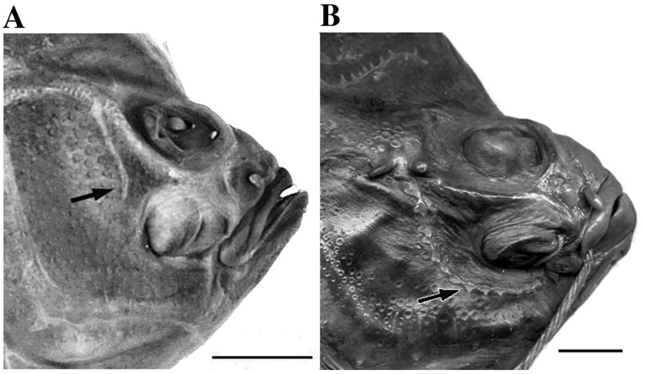

Figure 6. - Ocular side of the head. **A**: *Liopsetta putnami*, 177 mm SL. **B**: *Pleuronectes quadrituberculatus*, 375 mm SL. Arrow indicates infraorbital canal. Scale bar = 1 cm.

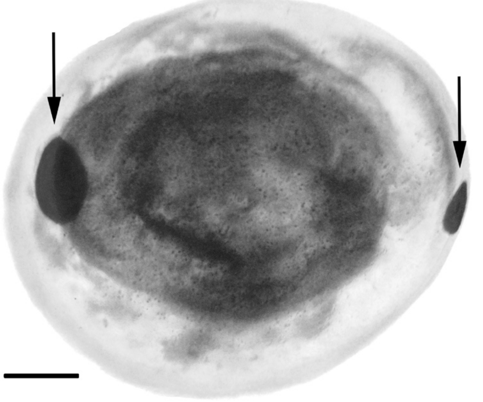

Figure 7. - Cleared and stained eye of *Liopsetta glacialis* (alizarin red). Arrows indicate scleral bones. Scale bar = 1 mm.

3. Species of the genus *Liopsetta* are the smallest among our sample of species (Tab. I). The use of size as a character can be controversial; there are numerous examples in teleost classification of close relatives with notably disjunct body size. Nevertheless maximum body size is used in the phylogenetic analysis, e.g. of Adrianichthyidae (Parenti, 2008). Regarding the maximum length of *L. pinnifasciata*, the original description of this species is based on the holotype of SL 215 mm ("Länge des beschriebenen Exemplares circa 8 Zoll") (Steindachner and Kner, 1870: 425). Authors of subsequent studies either just referred to the original description (Jordan and Goss, 1889; Jordan and Starks, 1907) or pointed out the maximum length of 250 mm on the basis of the original study (Schmidt, 1904). The maximum body size of this species is 350 mm, according to the reviews of the Far-East ichthyofauna (Schmidt, 1950; Moiseev, 1946; Fadeev, 2005) and papers on the biology of *L. pinnifasciata* (Pertseva-Ostroumova, 1961; Durkina, 2003; Durkina and Tcherkasova, 2007). These data do not corroborate the opinion that *L. pinnifasciata* attains 50 cm standard length (Masuda *et al*., 1984; Froese and Pauly, 2013; Nakabo, 2013).

Relationships of *Liopsetta*

According to the results of our phylogenetic analysis, three genera *Liopsetta*, *Pleuronectes* and *Pseudopleuronectes* are monophyletic (Fig. 1) and a close relationship between these genera as proposed earlier by Cooper and Chapleau (1998) is not supported. The present study shows that *Liopsetta* is more closely related to *Platichthys* than to *Pleuronectes*. It corroborates the hypothesis of pleuronectid genera relationships based on analyses of cytochrome *b* sequence data (Kartavtsev *et al*., 2007; Sharina and Kartavtsev, 2010) and DNA sequences from nuclear and mitochondrial genes (Roje, 2010).

Pseudopleuronectes appears to be the sister group of other genera studied here. A synapomorphy of this genus is the interrupted coronal commissure, resulting in two pores instead of one behind upper eye, that are noticeable in unstained specimens (Fig. 3B). This character state is rare for Pleuronectiformes and is evident only in *Pseudopleuronectes* and *Hippoglossoides* (Voronina, 2009; Voronina, unpubl. data).

The genera *Pleuronectes*, *Platichthys* and *Liopsetta* share one synapomorphy: the length of pyloric caeca is equal to or less than the diameter of the pyloric part of stomach (Norman, 1934; De Groot, 1971; Nikol'skaya and Verigina, 1974; Voronina and Evseenko, 2001). Pyloric caeca of *Verasper*, *Limanda* and *Pseudopleuronectes* are longer than twice the pyloric stomach diameter. These character states corroborate Storer's remark in his comparative description of *L. putnami* and *P. americanus*: "the difference in form of the caecal appendices, are very striking" (Storer, 1863: 245). The length of pyloric caeca compared to the diameter of the pyloric part of stomach is used in the present analysis instead of the number of pyloric caeca, traditionally used in the fish taxonomy. The number of pyloric caeca exhibits overlapping ranges of individual variation for the species studied (Norman, 1934), and thus it is difficult to use in analysis. *Pseudopleuronectes obscurus* shares characters, including an interrupted commissure, that we found in the genus *Pseudopleuronectes,* and it lacks synapomorphies of *Liopsetta*, confirming its appropriate placement within *Pseudopleuronectes*.

Pleuronectes is the sister group of the genera *Liopsetta*, *Platichthys* and *Limanda*. Two synapomorphies support the monophyly of this genus. The first synapomorphy, the radii completely surrounding the focus of scale, is revealed in species of *Pleuronectes* examined in the present study (Fig. 5). A photograph of a *P. platessa* scale at the ARKive web-site (http://www.arkive.org/european-plaice/pleuronectes-platessa/image-A23066.html) also shows this structure. It does not corroborate the coding of this character in the analysis of Cooper and Chapleau (1998), who referred to Batts (1964) as the source of their scale data. However Batts (1964) did not include *Pleuronectes*, *Liopsetta* and *Pseudopleuronectes* in his study of flatfish scales. The second synapomorphy is the absence of scleral ossicles (Fig. 7). Extensive investigation into their distribution in recent teleosts shows a consistent ossicle number in teleost families and the presence of a single anterior scleral ossicle in derived orders only (Franz-Odendaal, 2008). Scleral ossicle number varies from zero to two in Pleuronectiformes (Franz-Odendaal, 2008). The synapomorphies of *Pleuronectes* and *Liopsetta* support the hypothesis that these genera are distinct and with the states of six other characters readily distinguish these two genera.

Distribution and relationships among species of *Liopsetta*

The range of *L. glacialis* is Pacific high-boreal-Arctic (White Sea and Western coast of North America) according to modern range classifications (Chernova, 2011). Distribution of this species includes northern part of Sea of Ochotsk, Shantar Islands and Kamchatka Peninsula (Lindberg and Dulkeit, 1929; Sheiko and Fedorov, 2000; Fedorov *et al*., 2003). Distribution of *L. pinnifasciata* is Western Pacific low-boreal and includes Tartar Strait, Sea of Japan, Amur Bay, mouth of Amur River and off Sakhalin Island (Schmidt, 1904; Hubbs, 1915; Soldatov and Lindberg, 1930). The type location of this species – De Kastri Bay (Steindachner and Kner, 1870: 425). Jordan and Goss (1889: 290), referring to the original description, pointed out wrong distribution of *L. pinnifasciata* in 'Sea of Kamchatka, Decastris Bay'. Since that time Kamchatka has been mistakenly included into this species distribution in consequent reviews of local ichthyofauna (Jordan and Starks 1907; Sakamoto in Masuda *et al*. 1984; Amaoka *et al*. 1995; Nakabo, 2013). However, there is no evidence that *L. pinnifasciata* occurs in northern part of the Sea of Okhotsk (Sheiko and Fedorov, 2000; Fedorov *et al*., 2003) and reports of such occurrences have been questioned (Lindberg and Fedorov, 1993). The distribution of *L. putnami* is Western Atlantic high-boreal.

The morphometric variability of *L. glacialis* (Esipov, 1939; Probatov, 1940) is too low over the wide distribution range of this species to distinguish subspecies (Voronina and Evseenko, 2001; Yusupov and Basov, 2005). *Liopsetta pinnifasciata* differs from *L. glacialis* in having more pronounced bars on the median fins and in gill raker number, while the differences between these two species in the depth of body, morphology postocular ridge and lower pharyngeals (Hubbs, 1915; Norman, 1934) were not confirmed (Voronina and Evseenko, 2001). Both species are polymorphic in colour. In particular, we reidentified specimens of *L. pinnifasciata* from Kamchatka (ZIN 49985; Tokranov and Maksimenkov, 1995) as *L. glacialis*. There are one or two specimens with pronounced bars among many typically coloured specimens in trawl catches of *L. glacialis* off Kamchatka (Sheiko B.A., pers. comm.).

We found no differences in the external morphology between *L. putnami* and *L. glacialis*. However the differences in the type of egg and early development (Laroche, 1981), some meristics (Voronina and Evseenko, 2001) and allopatric distributions among these species keep them separate. There is no evidence that *L. glacialis*, *L. putnami* and *L. pinnifasciata* are conspecific, but the relationships of the three species of *Liopsetta* were incompletely resolved and require further investigations with genetic analysis.

Acknowledgments. – We express our sincere gratitude to Alexander M. Naseka (Zoological Institute RAS, St. Petersburg), Helmut Wellendorf (Naturhistorisches Museum Wien), Jeffrey T. Williams and Sandra J. Raredon (National Museum of Natural History, Washington) for taking photographs of type specimens and Galina A. Volkova and Elena M. Pavlova (Zoological Institute RAS, St. Petersburg) for their help. We are especially grateful for discussion of the parts of the manuscript with Boris Sheiko and Andre Bochkov (Zoological Institute RAS, St. Petersburg). This study was supported by the Fondation TOTAL (project "Classification des poissons marins: les téléostéens acanthomorphes") for B. Chanet. We would like to thank the two anonymous reviewers for their comments and for improving the English.

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APPENDIX I

List of character codes. This list includes description and comments of the character states. After the name of the character, the number assigned by Cooper and Chapleau (1998) is shown in parentheses. New characters and those with changed states are bold.

1. **Coronal commissure**. 0: not interrupted, connects canals of both side of the head; 1: interrupted, canals of sides of head are not connected.

2. **Infraorbital canal of ocular side** (8)**.** 0: developed; 1: reduced.

3. **Scleral ossicles**. 0: one or two bones present; 1: absent.

4. **Body scale size.** 0: equal or larger than lateral line scale; 1: half the size of lateral line scale.

5. **Structure of scales** (91). 0: radii extending anteriorly from focus of each scale; 1: radii completely surrounding focus of scale.

6. **Length of pyloric appendix.** 0: exceed the diameter of pyloric part of stomach more than twice; 1: equal or less diameter of pyloric part of stomach.

7. **Egg size.** 0: large, 1.0 mm in diameter or greater; 1: small, less than 1.0 mm in diameter (Table 1). Although polarity of egg size can be somewhat ambiguous, it was shown for some teleost groups that basal members have relatively large eggs (Parenti, 2008).

8. **Postanal pigment banding in pre- and flexion larvae**. 0: absent; 1: three and less; 2: heavy pigmentation (Table 1). This character is used in phylogenetic analysis of pleuronectid (Roje, 2010). However its state is miscoded for *Pleuronectes* and is changed in the present study.

9. **Maximum body size.** 0: 400 mm or larger; 1: 350 mm or less.

10. **Nasal bone on blind side** (50). 0: present; 1: absent. The character state is changed for *P. platessa*. Cooper and Chapleau (1998) pointed out the nasal bone absence in this species, however there is nasale with segment of supraorbital sensory canal (Cole and Johnstone, 1902; Voronina, 2002).

11. **Dorsal crest extending anteriorly from supraoccipital to blind-side frontal** (52). 0: prominent narrow crest present, angled laterally to ocular side; 1: reduced or absent crest resulting in a flattened posterior dorsal region on blind-side frontal. The character state is changed for *Pleuronectes platessa*, according to our observation of not prominent, but noticeable dorsal crest in this species.

12. Morphology of anterior prootic foramen, on ocular side (11). 0: sphenotic forms dorsal margin of foramen; 1: pterosphenoid and prootic join to form dorsal margin of foramen.

13. Bifurcation of first epibranchial (12). 0: distal end of first epibranchial divided into two branches; 1: distal end of first epibranchial simple.

14. Uniformity of dentition (16). 0: dentition of near equal or equal length; 1: teeth forming a continuous cutting edge.

15. Gill rakers on second epibranchial (30). 0: present; 1: reduced to just one gill raker at proximal base of epibranchial; 2: absent.

16. **Gill rakers on third epibranchial** (31). 0: reduced to just one gill raker at proximal base of epibranchial; 1: absent.

17. Articulation of blind-side metapterygiod with entopterygoid (34). 0: absent; 1: present.

18. **Cardiac apophysis of urohyal** (39). 0: cardiac apophysis is simple or slightly bifurcate at the posterior portion; 1: cardiac apophysis is strongly bifurcate at the posterior portion.

19. Gill rakers on fourth epibranchial (40). 0: absent; 1: present**.**

20. Rows of teeth in lower jaw (41). 0: multiserial or biserial rows of teeth. 1: uniserial row of teeth.

21. Supratemporals on ocular side (43). 0: supratemporal in one piece; 1: supratemporal in two pieces, jointed at anterior bifurcation point.

22. Supratemporals on blind side (44). 0: supratemporal in one piece. 1: supratemporal in two pieces, jointed at anterior bifurcation point.

23. **Rows of teeth on fifth ceratobranchial** (49). 0: regular two rows; 1: regular multiple rows or clustered.

24. Anterior margin of mesethmoid (53). 0: open canal extending from frontal on ocular side; 1: thin plate.

25. Asymmetry of size of space along ventral margin of dentary and articular (64). 0: space nearly the same size; 1: asymmetrical space, blind side greater than ocular side.

26. Asymmetry in size of dorsal posterior process of dentary (65). 0: symmetrical; 1: asymmetrical, ocular side greater than blind side.

27. Reduction of teeth on ocular-side maxilla (66). 0: number of teeth on ocular side nearly equal or equal to those on blind side; 1: ocular-side teeth fewer than blind- side teeth but greater than 6; 2: ocular-side teeth fewer than blind-side teeth, less than 6.

28. Reduction of teeth on ocular-side dentary (67) 0: number of teeth on ocular side nearly equal or equal to those on blind side; 1: ocular-side teeth fewer than blind-side teeth but greater than 6; 2: ocular-side teeth fewer than blind-side teeth, less than 6.

29. Epiotic process on ocular and blind sides (68). 0: process absent; 1: process is clearly evident extending anteriorly from epiotics onto parietals.

30. Shape of teeth (70). 0: sharply pointed; 1: bluntly conical or with truncated tips; 2: incisorlike.

31. Shape of fifth ceratobranchial (71). 0: straight «rod» shaped; 1: slight curve on medial margin; 2: strong curve on medial margin, the ceratobranchials forming or almost forming a triangular plate.

32. Dentition profile on fifth ceratobranchial (72). 0: pointed; 1: bluntly pointed; 2: rounded or molariform.

33. Egg type (75). 0: pelagic egg; 1: demersal egg.

34. Interpterosphenoid bar (98). 0: absent; 1: present.

35. Foramen on ocular-side dentary just below margin of dentition (99). 0: present; 1: absent.

36. Post-ocular ridge on blind side (100). 0: absent; 1: present.

37. Bony prominences along ocular-side postocular ridge (101). 0: absent. 1: many small bony prominences. 2: a series of enlarged prominences on postocular ridge.

38. Bony prominences along blind-side postocular ridge (102). 0: absent. 1: many small bony prominences present.

39. Bony plates or tubercles on body (105). 0: absent, 1: present.

40. Supratemporals fused to cranium (106). 0: not fused with cranium; 1: fused with cranium.

APPENDIX II

Matrix of 40 morphological characters for 15 pleuronectid taxa. Numbers in the matrix represent character state as described in Appendix I. Question marks (?) indicate an unknown state.

Taxon	Character																																						
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Verasper variegatus	0	0	0	0	0	0	0	2	0	0	0	1	1	0	2	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Limanda aspera	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	1	0	0	0	1	1	1	0	2	1	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0
L. limanda	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	1	1	0	0	1	0	0	0	2	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
L. proboscidea	0	0	0	0	0	0	1	1	0	1	1	0	1	1	0	1	1	0	0	1	0	0	0	2	1	1	1	1	1	1	1	1	0	1	0	1	1	1	0	0
Pseudopleuronectes americanus	1	0	0	0	0	0	1	1	0	1	1	0	1	2	1	1	1	1	0	1	0	0	0	1	0	0	2	2	0	2	1	1	1	1	1	1	0	0	0	0
P. herzensteini	1	0	0	0	0	0	1	1	0	1	1	1	1	2	1	1	1	0	1	0	0	0	0	1	0	0	2	2	1	2	1	1	0	0	0	1	0	0	0	0
P. yokohamae	1	0	0	0	0	0	1	1	0	1	1	1	1	2	1	1	1	1	0	1	0	0	0	1	1	1	2	2	0	2	1	1	1	1	1	1	0	0	0	0
P. obscurus	1	0	0	0	0	0	1	1	0	1	1	1	1	2	1	0	1	1	1	1	1	1	0	1	0	1	2	2	1	2	1	2	1	0	1	1	1	0	0	0
Pleuronectes platessa	0	0	1	0	1	1	0	0	0	0	0	1	1	2	1	2	1	1	0	1	1	1	1	1	1	1	2	2	1	2	2	2	0	1	0	1	2	0	0	0
P. quadrituberculatus	0	0	1	0	1	1	0	0	0	0	0	1	1	2	1	0	1	1	0	1	1	1	0	1	1	1	2	2	1	2	1	1	0	1	0	1	2	0	0	0
Liopsetta glacialis	0	1	0	1	0	1	0	1	1	0	0	1	1	2	1	1	1	1	0	1	0	0	1	3	1	0	2	1	1	2	2	2	0	1	0	1	1	1	0	0
L. pinnifasciatus	0	1	0	1	0	1	0	1	1	0	0	1	1	2	1	1	1	1	0	1	0	0	1	3	1	0	2	2	1	2	2	2	0	1	0	1	1	1	0	0
L. putnami	0	1	?	1	0	1	0	1	1	0	0	1	1	2	1	1	1	1	0	1	0	0	1	3	1	0	2	1	1	2	2	2	1	1	0	1	1	0	0	0
Platichthys flesus	0	0	0	0	2	1	0	1	0	0	1	1	1	1	2	2	1	1	0	1	0	0	1	3	1	1	1	1	1	1	2	1	0	1	1	1	1	1	1	1
P. stellatus	0	0	0	0	2	1	0	1	0	0	1	0	1	1	2	2	1	1	0	1	0	0	1	3	1	1	1	1	1	1	2	1	0	1	0	1	1	1	1	1